

Social-Cognitive Deficits in Normal Aging

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A sizeable number of studies have implicated the default network (e.g., medial prefrontal and parietal cortices) in tasks that require participants to infer the mental states of others (i.e., to mentalize). Parallel research has demonstrated that default network function declines over the lifespan, suggesting that older adults may show impairments in social-cognitive tasks that require mentalizing. Older and younger human adults were scanned using functional magnetic resonance imaging while performing three different social-cognitive tasks. Across three mentalizing paradigms, younger and older adults viewed animated shapes in brief social vignettes, stories about a person's moral actions, and false belief stories. Consistent with predictions, older adults responded less accurately to stories about others' false beliefs and made less use of actors' intentions to judge the moral permissibility of behavior. These impairments in performance during social-cognitive tasks were accompanied by age-related decreases across all three paradigms in the BOLD response of a single brain region, the dorsomedial prefrontal cortex. These findings suggest specific task-independent age-related deficits in mentalizing that are localizable to changes in circumscribed subregions of the default network.

Introduction

Social interaction is one of the most difficult businesses in which humans involve themselves. Predicting the actions of people with whom we interact, while they predict ours, presents challenges qualitatively distinct from those encountered in the physical world. In recent years, researchers have amassed considerable evidence that a similarly distinct set of brain regions is associated with "mentalizing," the psychological process used to understand what others are thinking or feeling (Saxe et al., 2006a; Van Overwalle, 2009). Chief among these regions are cortical midline structures, such as medial prefrontal cortex (MPFC) and posterior cingulate cortex (PCC), as well as the temporoparietal junction (TPJ) and superior temporal sulcus (STS) (Adolphs, 2001).

Interestingly, many of these regions are also major nodes in the "default network," which comprises a functionally interconnected set of regions with tonically high resting activity (Raichle et al., 2001). Changes in activity across different nodes of this network tend to co-occur, such that increases in one region (e.g., MPFC) are accompanied by increases in other regions of the network (e.g., PCC). However, recent work has revealed substantial declines in such functional connectivity during normal aging, such that older adults demonstrate smaller correlations in resting activity across regions of the default network (Andrews-Hanna et al., 2007; Damoiseaux et al., 2008). Moreover, these declines in connectivity are associated with other biological markers of the

onset of Alzheimer's disease, such as amyloid β plaques (Buckner et al., 2005; Hedden et al., 2009; Sheline et al., 2010).

To the extent that mentalizing relies on the default network, these observations suggest that normal aging may be associated with concomitant declines in the ability to understand other minds. To test this hypothesis, we used functional magnetic resonance imaging (fMRI) to scan older and younger adults while they completed a battery of social-cognitive tasks. These tasks varied in the extent to which they explicitly required participants to represent others' mental states and to which they placed demands on working memory and verbal processing. Within the literature on the effects of aging on memory, a range of findings suggest that older adults show especially pronounced deficits when required to initiate mnemonic retrieval themselves (e.g., during recall), but that they often show intact performance on tasks that explicitly guide retrieval (e.g., recognition tasks) (Craik, 1983; Parkin and Walter, 1992; Daselaar et al., 2006). Here, we examined whether older adults might likewise demonstrate particularly pronounced social-cognitive impairments when required to initiate such processing spontaneously. To this end, we included tasks that directed participants to consider others' mental states (false belief task), as well as tasks that required spontaneous engagement of social-cognitive processing (moral judgment and animate movement tasks). Moreover, research has suggested that aging-related changes in working memory may account for deficits in social cognition among older adults. To examine this possibility, the current tasks varied in their working memory demands. Across task variations, we hypothesized that older adults would demonstrate a consistent impairment in social-cognitive performance, which would be linked to down-regulation of specific components of the default network, such as the MPFC.

Materials and Methods

Participants. Thirty-one younger [age: (mean \pm SEM) 23.0 \pm 0.9 years; 12 male] and 17 older (age: 71.8 \pm 1.9 years; nine male) adults partici-

Received Nov. 1, 2011; revised Feb. 8, 2012; accepted Feb. 28, 2012.

Author contributions: J.M.M. and J.P.M. designed research; J.M.M. and E.J. performed research; J.M.M. and E.J. analyzed data; J.M.M. and J.P.M. wrote the paper.

This work was supported by a grant from the National Institute for Aging (R01AG032780-01) and the Office of Behavioral and Social Sciences Research. We thank Randy Buckner for helpful advice and Diana Bartenstein for assistance.

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DOI:10.1523/JNEUROSCI.5511-11.2012

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pated in exchange for payment. Informed consent was obtained in a manner approved by the Committee on the Use of Human Subjects at Harvard University. Older participants were screened using the Mini Mental State Examination [score: mean (M) = 29.6; range = 27–30]. For the false belief and moral judgment tasks, data from two older participants were excluded due to excessive between-scan movement (>1 mm). One additional older participant was claustrophobic, and hence completed versions of the moral judgment and false belief tasks outside the scanner. Due to time constraints, some of the younger participants did not complete all three neuroimaging paradigms. In sum, imaging data are reported according to the following counts: animate movement, 28 younger, 16 older; moral judgment; 27 younger, 14 older; false belief, 29 younger, 14 older. Further, behavioral data were not collected from two older participants due to equipment malfunction. Accordingly, behavioral data are reported according to the following counts: moral judgment, 27 younger, 14 older; false belief, 29 younger, 13 older (participants did not respond behaviorally during the animate movement task).

Behavioral procedure. Participants were scanned while completing three tasks that have been used extensively to examine mentalizing and social cognition: (1) animate movement, (2) moral judgment, and (3) false belief. During the animate movement task (Heider and Simmel, 1944; Martin and Weisberg, 2003), participants viewed short movies that depicted animated geometric shapes performing social and mechanical actions (e.g., friends sharing ice cream or a cannon firing). Hence, movies across the two conditions contained similar information (colored geometric shapes), but differed on whether they communicated information about social interactions or a mechanical scene. Participants were simply instructed to attend to each movie, and were not required to make behavioral responses. Sixteen movies (eight social, eight mechanical) were presented in a pseudorandomized order during a single functional run (243 time points). Movies were 20–25 s in duration ($M = 21$ s), and were buffered with an additional period of passive fixation such that each trial lasted for 30 s total. Trials were modeled as blocks (epochs) for the length of the movie.

During the moral judgment task (Young et al., 2007), participants read stories that described an ambiguous moral action and rated the moral permissibility of the behavior. In each story, an actor performed an action with either a neutral or negative intent (e.g., putting powder in a cup to sweeten someone's coffee or to poison someone) and either a neutral or a negative outcome (e.g., the drinker was either unharmed or harmed by the action; see Moran et al., 2011, for examples). Each story was presented in five segments: (1) expository information that provided a background scene (14 s); (2) a foreshadow segment that provided information as to whether the outcome would be neutral or negative (10 s); (3) intention information that described the actor's neutral or negative intent (10 s); (4) outcome information that described the neutral or negative result (10 s); and finally, (5) the judgment segment, during which participants rated the moral permissibility of the actor's behavior (8 s). For example, "Grace and her friend are taking a tour of a chemical plant. When Grace goes over to the coffee machine to pour some coffee, Grace's friend asks for some sugar in hers. There is white powder in a container by the coffee. The white powder is a very toxic substance left behind by a scientist, and therefore deadly when ingested in any form. The container is labeled 'sugar,' so Grace believes that the white powder by the coffee is sugar left out by the kitchen staff. Grace puts the substance in her friend's coffee. Her friend drinks the coffee and dies." The nature of the actor's intention (neutral, negative) and the outcome (neutral, negative) varied orthogonally across stories, resulting in four types of trials: neutral-intention/neutral-outcome; neutral-intention/negative-outcome; negative-intention/neutral-outcome; and negative-intention/negative-outcome. This task tests the extent to which participants spontaneously engage in mentalizing, as perceivers must consider the actor's mental state to judge whether someone who accidentally causes harm deserves punishment (neutral intention leading to a negative outcome) or to judge whether someone should be punished for an act with harmful intent but without a harmful outcome (negative intention leading to a neutral outcome) (Young et al., 2007; Moran et al., 2011). Successful mentalizing during this task is reflected in rating accidental harm to be more permissible

(since the actor did not intend to harm, as in manslaughter) and in rating failed attempts to harm to be less permissible (since the actor had intended to harm another person, as in attempted murder). Six trials of each type were presented across four functional runs (189 time points per run). Participants rated the permissibility of each action on a five-point scale from least to most permissible, using a response box in their right hand. Trials were modeled as blocks (epochs) from the phase in which participants were shown the intention information.

During the false belief task, participants answered questions about stories that referred either to a person's false belief (mental trials) or to outdated physical representations, such as an old photograph (physical trials; Zaitchik, 1990; Saxe and Kanwisher, 2003). For example: "Jenny put her chocolate away in the cupboard. Then she went outside. Alan moved the chocolate from the cupboard into the fridge. Half an hour later, Jenny came back inside"; or "A photograph was taken of an apple hanging on a tree branch. The film took half an hour to develop. In the meantime, a strong wind blew the apple to the ground." Each trial began with a story presented for 10 s, which was followed (after a variable delay of 0–6 s) by a question for 6 s. Twelve stories of each type were presented across two functional runs (179 time points per run). Trials were modeled as blocks (epochs) for the story phase.

Imaging procedure. Functional data for all tasks were acquired using a gradient-echo echo-planar pulse sequence ($TR = 2$ s; $TE = 35$ ms) on a 3T Tim Trio MRI scanner (Siemens). Images were acquired using 36 axial, interleaved slices with a thickness of 3 mm (0.54 mm skip) and 3×3 mm in-plane resolution. Functional images were preprocessed and analyzed using SPM8 (Wellcome Department of Cognitive Neurology) and custom software (spm8w, Dartmouth College). Data were realigned within and across runs to correct for head movement, were unwarped to correct for geometric distortions, and were transformed into a standard anatomical space (2 mm isotropic voxels) based on the ICBM-152 brain template [Montreal Neurological Institute (MNI)]. Normalized data were then spatially smoothed (8 mm full width at half maximum) using a Gaussian kernel. Finally, using custom artifact detection software (http://www.nitrc.org/projects/artifact_detect), individual runs were analyzed on a participant-by-participant basis to find outlier time points. Specifically, we excluded volumes during which participant head motion exceeded 0.5 mm or 1° and volumes in which the overall signal for that time point fell >3 SDs outside the mean global signal for the entire run. Outlier time points were excluded from the GLM analysis via the use of participant-specific regressors of no interest.

For all tasks, preprocessed images were analyzed using a general linear model in which trials were modeled as blocks. Trials were modeled using a canonical hemodynamic response function and covariates of no interest (session mean and linear trend, outlier time points excluded as indicated above). Analysis was performed individually for each participant, and contrast images were subsequently entered into second-level analyses, treating participants as a random effect. Peak coordinates were identified at the group level using a statistical criterion of 56 or more contiguous voxels at a voxelwise threshold of $p < 0.005$, providing an experiment-wise threshold of $p < 0.05$, corrected for multiple comparisons [threshold determined by Monte Carlo simulations (Slotnick et al., 2003)].

Results

Animate movement task

During the animate movement task, participants passively viewed animations of colored geometric shapes that were either social or mechanical in nature. Participants were not required to make behavioral responses during this task. Analysis of fMRI data first identified neural regions in which BOLD response differentiated social from mechanical vignettes. Whole-brain statistical maps were created from contrast between images captured during social vignettes and images captured during mechanical vignettes (social vs mechanical) for each participant group separately (one-sample t test). In younger adults, this contrast revealed a set of regions identified by earlier research using these same stimuli (Martin and Weisberg, 2003), including bilateral

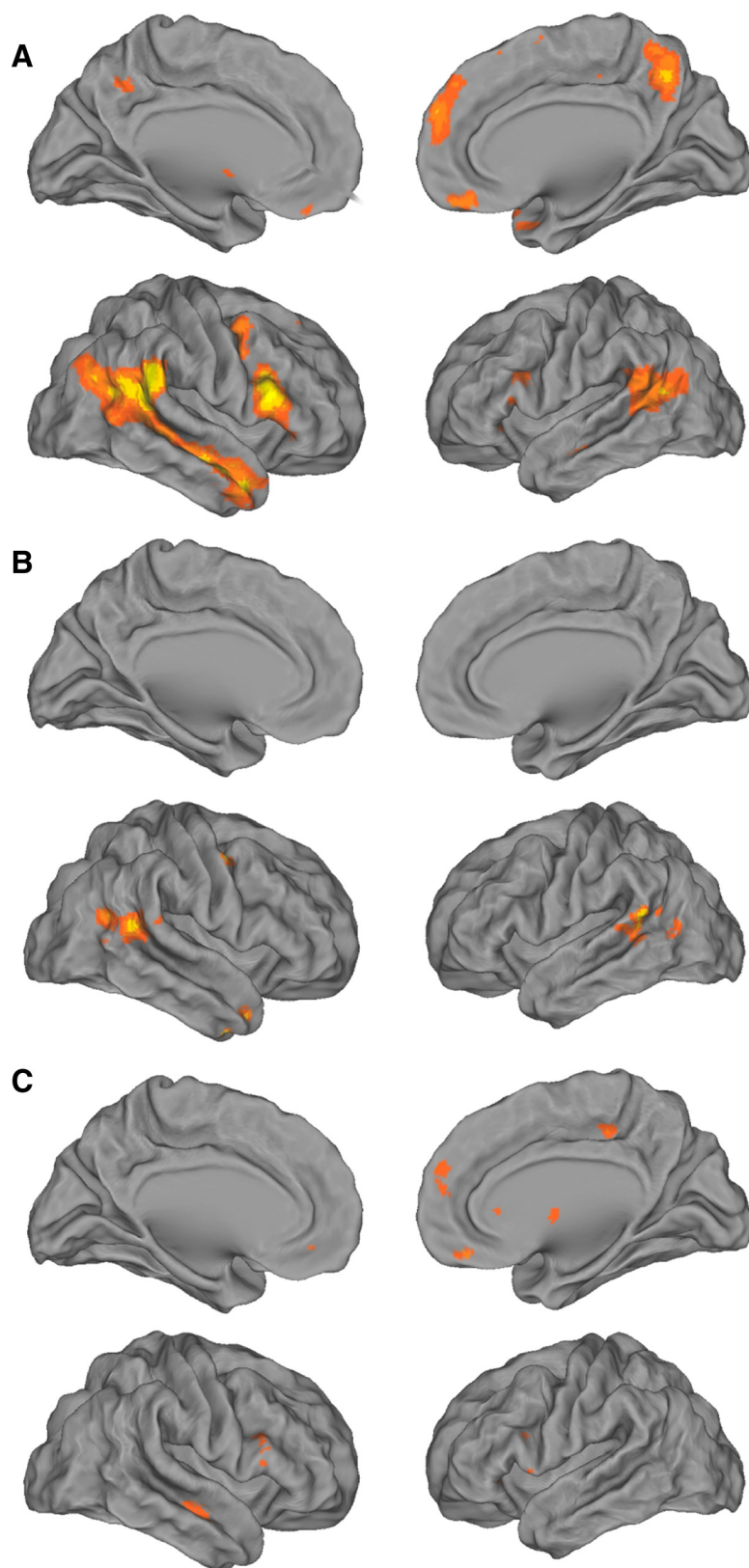


Figure 1. *A, B*, Regions showing significantly greater BOLD responses to social–mechanical movies during the animate movement task (corrected $p < 0.05$), separately for (*A*) younger and (*B*) older adults. Coordinates are displayed in Table 1. *C*, A direct comparison of these effects across age groups revealed that young participants showed significantly greater activation than older adults in ventral and dorsal medial prefrontal cortex, bilateral inferior frontal gyrus, right superior temporal sulcus, and the putamen.

TPJ, anterior STS, and ventral MPFC, as well as dorsal MPFC, precuneus, and bilateral inferior frontal gyrus (IFG) (Fig. 1*a*). In older adults, this contrast revealed differences only in bilateral TPJ, the precuneus, right IFG, and the temporal pole (Fig. 1*b*). A direct contrast of the two groups of participants revealed significantly greater activity among younger adults (relative to older adults) in several regions, including ventral and dorsal MPFC, bilateral IFG, and right anterior STS (Fig. 1*c*). Details of neural differences are reported in Table 1.

Moral judgment task

During the moral judgment task, participants were asked to judge the permissibility of an actor's actions on the basis of his or her intention (neutral, negative) and the outcome (neutral, negative). We first compared older and younger adults' permissibility ratings for neutral outcomes as a function of whether actors had neutral or negative intentions. Overall, participants rated neutral outcomes brought about by negative intentions as less permissible than those brought about by neutral intentions [$F_{(1,39)} = 153.36$, $p < 0.001$, Cohen's $d = 1.98$]. However, this main effect was qualified by a significant age–intention interaction [$F_{(1,39)} = 4.98$, $p < 0.05$, Cohen's $d = 0.71$] such that older adults placed relatively less emphasis on actors' negative intentions when rating the permissibility of actions (Fig. 2, left). That is, compared with younger participants, older adults judged an actor's behavior to be relatively permissible if it resulted in a neutral outcome despite the actor's negative intentions, suggesting that older adults attended less to information about the actor's negative intention than to the outcome itself when assigning blame. Next, we compared permissibility ratings of older adults with those of younger adults for negative outcomes as a function of actors' intentions. This analysis was intended to determine whether the moral judgments of older adults likewise differed from those of younger adults when actions caused negative outcomes. Such a finding would suggest that aging-related changes in moral judgment are independent of the outcome of the action, and more likely the result of deficits in the use of theory-of-mind among older adults. As for neutral outcomes, participants overall rated negative acts brought about by negative intentions as less permissible than those brought about by neutral intentions [$F_{(1,39)} = 111.75$, $p < 0.001$, Cohen's $d =$

Table 1. Peak voxel and cluster size for regions obtained from the contrast of social–mechanical movies in the animate movement task

Anatomic label	x	y	z	Peak <i>t</i>	Voxel extent
Young adults					
Dorsal medial prefrontal cortex	8	59	28	4.25	423
	8	61	18	3.72	
Ventral medial prefrontal cortex	4	43	−18	4.31	182
Inferior frontal gyrus	−48	19	18	4.31	276
	42	23	22	6.27	1254
	48	23	16	6.17	
	46	31	−4	3.95	
Globus pallidus	18	1	0	3.70	58
Middle frontal gyrus	34	1	38	5.16	440
Superior temporal sulcus	54	−1	−18	3.69	160
	50	−3	−18	3.17	
Precuneus	4	−57	48	3.98	656
	12	−51	36	2.89	
Temporoparietal junction	−62	−59	22	4.94	2121
	−56	−71	18	4.87	
	−46	−59	16	4.69	
	60	−45	16	6.39	4746
	48	−51	22	6.00	
	52	−41	14	5.96	
Older adults					
Temporal pole	44	13	−34	5.51	78
Precentral gyrus	52	3	50	5.63	118
Temporoparietal junction	−60	−47	18	5.48	366
	−62	−35	12	4.28	
	46	−45	26	5.83	937
	46	−47	12	5.30	
	40	−59	22	4.99	
Middle temporal gyrus	−40	−63	12	3.55	138
Young versus older					
Dorsal medial prefrontal cortex	−6	59	24	3.67	434
	10	59	16	3.40	
	4	59	24	3.36	
	−8	33	44	3.62	178
Ventral medial prefrontal cortex	4	43	−18	4.18	95
Middle frontal gyrus	22	31	40	3.68	68
Inferior frontal gyrus	−48	21	18	3.39	149
	44	25	18	4.00	411
	54	23	20	3.34	
Putamen	20	5	0	4.05	229
Superior temporal sulcus	56	−9	−16	3.79	163
Older versus young					
No significant voxels					

Stereotaxic coordinates reported according to the Montreal Neurological Institute coordinate system.

1.69]. This main effect was again qualified by a significant age–intention interaction [$F_{(1,39)} = 6.37, p < 0.02$, Cohen's $d = 0.81$] such that older adults placed relatively less emphasis on actors' intentions (Fig. 2, right). That is, compared with younger participants, older adults judged an actor's behavior to be less permissible if it resulted in a negative outcome despite the actor's benign intentions, again suggesting that older adults attended less to information about the actor's intention than to the outcome. We observed no main effect of age for either neutral outcomes [$F_{(1,39)} = 1.16, p = 0.29$, Cohen's $d = 0.34$] or negative outcomes [$F_{(1,39)} = 1.02, p = 0.32$, Cohen's $d = 0.32$]. Together, these results suggest that older adults did not spontaneously engage in mentalizing to the same degree as did younger adults during judgments of moral permissibility. Finally, we observed no main effect of age on reaction times [$F_{(1,39)} = 2.48, p > 0.1$], and no interactions with age–intention [$F_{(1,39)} = 2.50, p > 0.1$]; age–outcome ($F < 1$); and age–intention–outcome ($F < 1$).

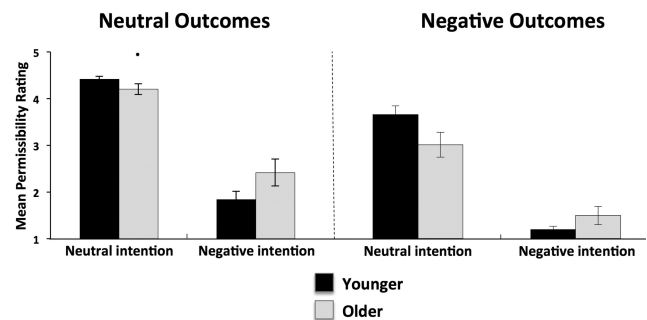


Figure 2. Permissibility ratings during the moral judgment task. Left, Permissibility ratings for neutral outcomes, as a function of whether actors had neutral (left) or negative (right) intentions. Right, Permissibility ratings for negative outcomes as a function of these intentions. In judging whether a person performing an act with harmful intent should be punished, even if the outcome created no harm, older adults were less likely than their younger counterparts to take into account the person's intentions. Older adults were similarly less likely than their younger counterparts to take into account the person's intentions in judging whether a person performing a harmful act should be punished, even if that person had no harmful intent.

Analysis of fMRI data extended these behavioral findings by comparing instances where participants must engage in mentalizing because intentions and outcomes conflict with one another (e.g., neutral-intention/negative-outcome) versus instances where participants need not richly mentalize because intentions and outcomes match (e.g., neutral-intention/neutral-outcome). This analysis was performed for both neutral and negative intentions separately. Accordingly, our first analysis of fMRI data identified neural regions in which BOLD response differentiated neutral-intention/negative-outcome from neutral-intention/neutral-outcome stories. In younger adults, this contrast revealed a set of regions identified by earlier research using these same stimuli (Young et al., 2007), including bilateral TPJ, ventral and dorsal MPFC, and the right temporal pole (Fig. 3*a*). In older adults, significantly greater activation was seen in the TPJ, precuneus, and the supplementary motor area (Fig. 3*b*). A direct contrast of the two age groups revealed greater activation in the right ventral and dorsal MPFC for younger than for older adults—consistent with findings from the animate movement task—as well as in the pulvinar (Fig. 3*c*). Details of neural differences are reported in Table 2*a*. In the second analysis, we identified neural regions in which BOLD response differentiated negative-intention/neutral-outcome from negative-intention/negative-outcome stories. In younger adults, this contrast observed activation solely in the middle orbital gyrus. In older adults, there were no areas of greater activation. A direct contrast of the two age groups revealed greater activation in the middle temporal gyrus, thalamus, and lingual gyrus. Details of neural differences are reported in Table 2*b*.

False belief task

During the false belief task, participants answered questions about either false beliefs or outdated physical representations (false photos). Overall, participants more accurately answered questions about false belief stories ($M_{\text{proportion}} = 0.91$) than false photo stories ($M = 0.79$) [$F_{(1,40)} = 9.77, p < 0.003$, Cohen's $d = 0.49$] (Fig. 4*a*), and this main effect was qualified by a marginally significant age–story-type interaction [$F_{(1,40)} = 3.28, p = 0.08$, Cohen's $d = 0.57$], which resulted from a difference in accuracy across story types among older adults. Specifically, older participants answered marginally fewer false belief questions correctly ($M = 0.85$) than did younger participants [$M = 0.94, t_{(40)} = 1.98, p = 0.054$, Cohen's $d = 0.63$], but the

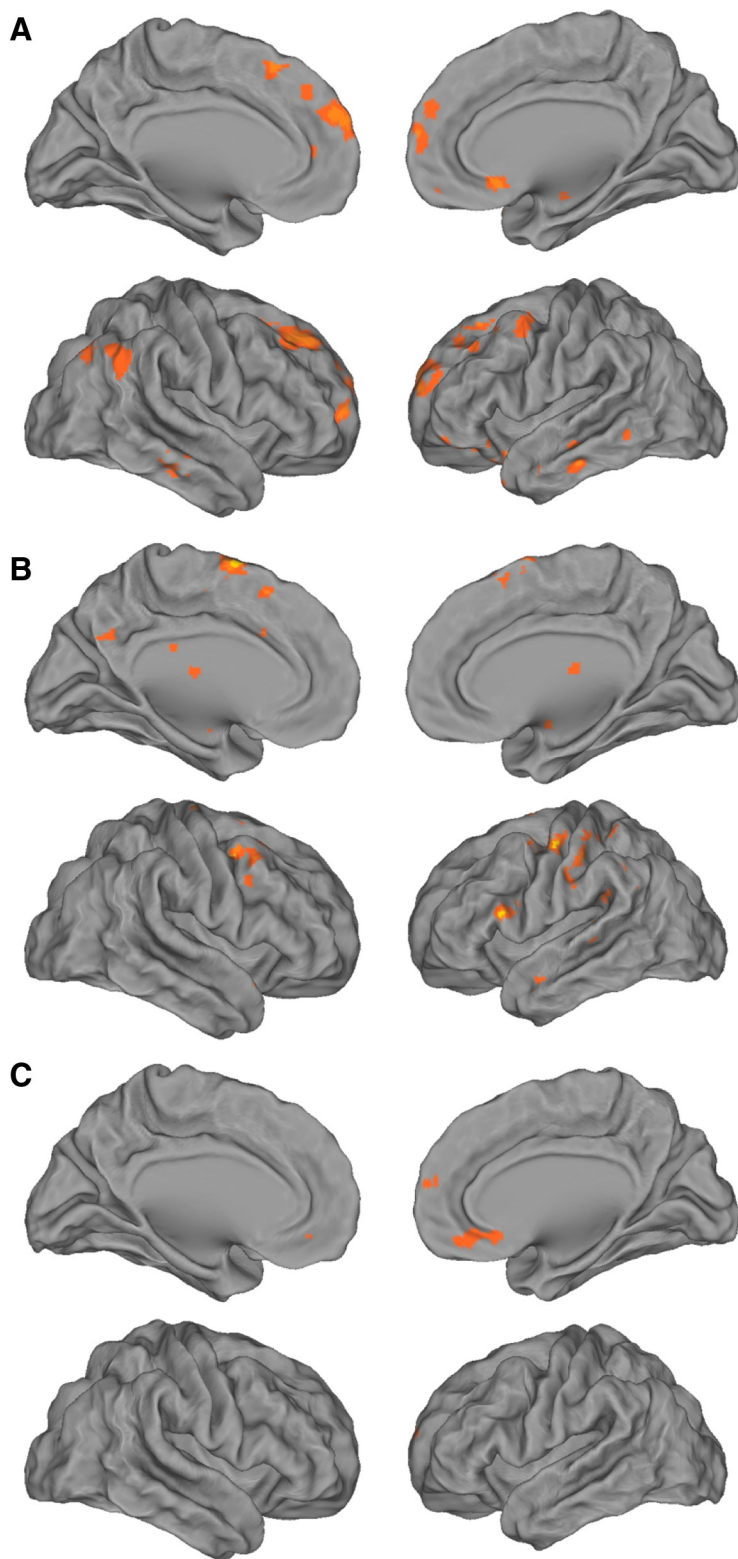


Figure 3. *A, B*, Regions showing significantly greater BOLD response to neutral-intention/negative-outcome–neutral-intention/neutral-outcome stories (corrected $p < 0.05$), separately for younger (*A*) and older (*B*) adults. Coordinates are displayed in Table 2a. *C*, A direct comparison of these effects across age groups revealed that young adults showed significantly greater activation than older adults in ventral and dorsal medial prefrontal cortex.

two groups answered a similar proportion of false photo questions correctly (81 vs 79%, respectively). Intriguingly, we observed a significant negative correlation between age and performance on the false belief stories among older adults [$r_{(11)} = -0.68, p < 0.01$], such

that the oldest participants performed worst on the false belief stories (Fig. 4*b*). Importantly, no significant correlation was observed between age and performance on the false photo stories [$r_{(11)} = 0.28, p > 0.10$], and these correlations were significantly different from one another (Fisher r to z transformation: $z = -2.50, p < 0.02$), demonstrating that the effect of age on performance was specific for social-cognitive processing during the false belief stories. Additionally, we observed a main effect of age on reaction time [$F_{(1,40)} = 18.75, p < 0.001$], but no age–story-type interaction ($F < 1$).

Analysis of fMRI data first identified neural regions in which BOLD response differentiated false belief from false photo stories. Whole-brain statistical maps were created from the false belief–false photo contrast for each participant group separately (one-sample t test). In younger adults, this contrast revealed a set of regions identified in several papers using these same stimuli (Saxe and Kanwisher, 2003; Saxe et al., 2006*b*), including bilateral TPJ, precuneus, anterior STS, and dorsal MPFC (Fig. 5*a*). In older adults, this contrast revealed greater activation in the precuneus and right TPJ only (Fig. 5*b*). A direct contrast of the two age groups again revealed significantly greater activation among younger adults (relative to older adults) in a single region of dorsal MPFC, consistent with findings from both the animate movement and moral judgment tasks (Fig. 5*c*). Details of neural differences are reported in Table 3.

Overall conjunction and region-of-interest analyses

Analysis of each of the three tasks separately suggests that older adults show consistent differences from and younger adults in neural activation during social-cognitive tasks, and that these differences primarily involve the MPFC. To test whether these differences occurred in the very same region across tasks, we performed a formal conjunction analysis that identified voxels common to the difference between younger and older adults for each of the tasks: that is, social–mechanical animations, negative-intention/neutral-outcome–negative-intention/negative-outcome and neutral-intention/negative-outcome–neutral-intention/neutral-outcome moral scenarios, and false belief–false photo stories.

This analysis was performed using the minimum statistic for conjunction null method (Nichols et al., 2005), resulting in an overall α of $p < 0.05$. For the moral judgment task, an inclusive (OR) composite image (in which activations surviving the threshold in either of the two con-

Table 2. Peak voxel and cluster size for all regions obtained from (a) the contrast of neutral-intention/negative–neutral-intention/neutral outcome stories, and (b) the contrast of negative-intention/neutral–negative-intention/negative outcome in the moral judgment task

Anatomic label	x	y	z	Peak t	Voxel extent
(a) Neutral-intention/negative–neutral-intention/neutral outcome					
Young adults					
Superior frontal gyrus	20	63	16	4.45	3656
Dorsal medial prefrontal cortex	–16	31	54	4.40	
	–6	59	28	4.33	
Middle orbital gyrus	–24	25	–12	3.60	
Ventral medial prefrontal cortex	8	25	–10	4.07	162
	0	27	–14	3.53	
Amygdala	–18	–1	–18	4.86	335
Inferior temporal gyrus	–56	–23	–20	3.88	255
	–58	–19	–12	3.84	
Parahippocampal gyrus	–20	–25	–16	3.01	72
Superior temporal sulcus	66	–27	–16	3.72	150
Temporoparietal junction	–56	–65	24	3.75	65
Angular gyrus	46	–71	42	4.00	642
	62	–53	32	3.90	
	56	–55	40	3.69	
Older adults					
Dorsal medial prefrontal cortex	–4	21	54	3.93	109
Middle frontal gyrus	44	5	50	4.95	147
Precentral gyrus	–44	–9	56	5.05	646
Supplementary motor area	–4	7	70	5.74	412
Transverse temporal gyrus	–42	–33	10	5.35	66
Supramarginal gyrus	–48	–37	32	5.09	479
Angular gyrus	62	–55	32	3.94	88
Temporoparietal junction	54	–69	22	3.82	93
Amygdala	24	–1	–14	4.00	88
Thalamus	4	–15	12	4.26	299
Young versus older					
Dorsal medial prefrontal cortex	18	61	16	3.96	165
	–12	65	20	3.50	75
Ventral medial prefrontal cortex	12	41	–12	3.65	94
Older versus young					
Precentral gyrus	–46	–11	54	3.70	1610
Thalamus	–12	–17	14	3.87	430
Superior parietal lobule	18	–49	62	3.56	338
(b) Negative-intention/neutral–negative-intention/negative outcome					
Young adults					
Middle orbital gyrus	42	51	–12	4.83	93
Older adults					
No significant voxels					
Young versus older					
Thalamus	20	–27	0	4.12	418
Middle temporal gyrus	54	–37	–8	4.18	89
Lingual gyrus	14	–85	–18	3.32	66
Older versus young					
No significant voxels					

Stereotaxic coordinates reported according to the Montreal Neurological Institute coordinate system.

trasts would emerge in the composite image) was first created for both contrasts. This image was compared with those from animate movement and false beliefs tasks in an exclusive (AND) conjunction analysis. This analysis revealed that a single brain region—located in dorsal MPFC (MNI coordinates: $x/y/z = 10, 61, 18$)—was more active in younger adults than in older adults during all three social-cognitive paradigms (Fig. 6a), suggesting that this region may in part be responsible for reduced mentalizing in the older adults.

Discussion

Across a range of social-cognitive tasks, older adults demonstrated a consistent deficit in processing the mental states of others. Com-

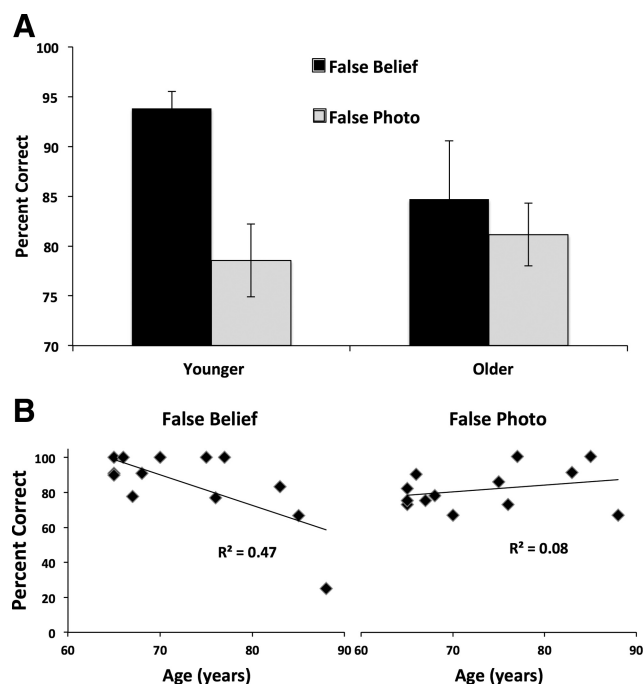


Figure 4. *A*, Accuracy during the false belief task. Both younger and older participants performed better on false belief than false photo questions, but older adults correctly answered fewer false belief questions correctly than did younger participants ($p = 0.054$). *B*, For older participants, there was a significant negative correlation between age and the number of correctly answered questions about false beliefs but not about false photographs.

pared with younger participants, older adults less often took mental states (intentions) into account when making judgments of moral permissibility and less often correctly appreciated others' false beliefs. Such differences were not observed on nonsocial versions of these tasks that made similar working memory and verbal demands but did not require participants to understand another person's mental states (e.g., during false photograph trials).

Parallel to these aging-related decrements in performance on social-cognitive tasks were similar decreases in the response during these tasks of a single brain region, dorsal MPFC. Consistent with a large number of earlier studies, younger adults demonstrated considerable engagement of this region during social-cognitive—compared with nonsocial—tasks (Kelley et al., 2002; Mitchell et al., 2005). In contrast, older adults consistently failed to engage this region across these disparate types of social tasks. The downregulation of dorsal MPFC was observed regardless of the extent to which the task explicitly prompted participants to consider others' mental states and the extent to which the task taxed working memory or verbal processing. In this regard, social cognition appears unlike some other psychological skills. For example, older adults typically show substantially worse episodic memory on unconstrained tasks that do not expressly guide retrieval (such as free recall) than on those that direct memory in a particular way (such as recognition) (Craik, 1983; Logan et al., 2002; Gutchess et al., 2007b). In contrast, we observed no such differences across social-cognitive tasks: older adults showed less MPFC response and decreased performance even during social-cognitive tasks that explicitly asked them to infer others' mental states, such as during the false belief task. Likewise, aging-related neural differences were unaffected by whether tasks required verbal processing or might have required working memory: older adults demonstrated diminished MPFC response even during social-cognitive tasks that simply asked them to watch visual dis-

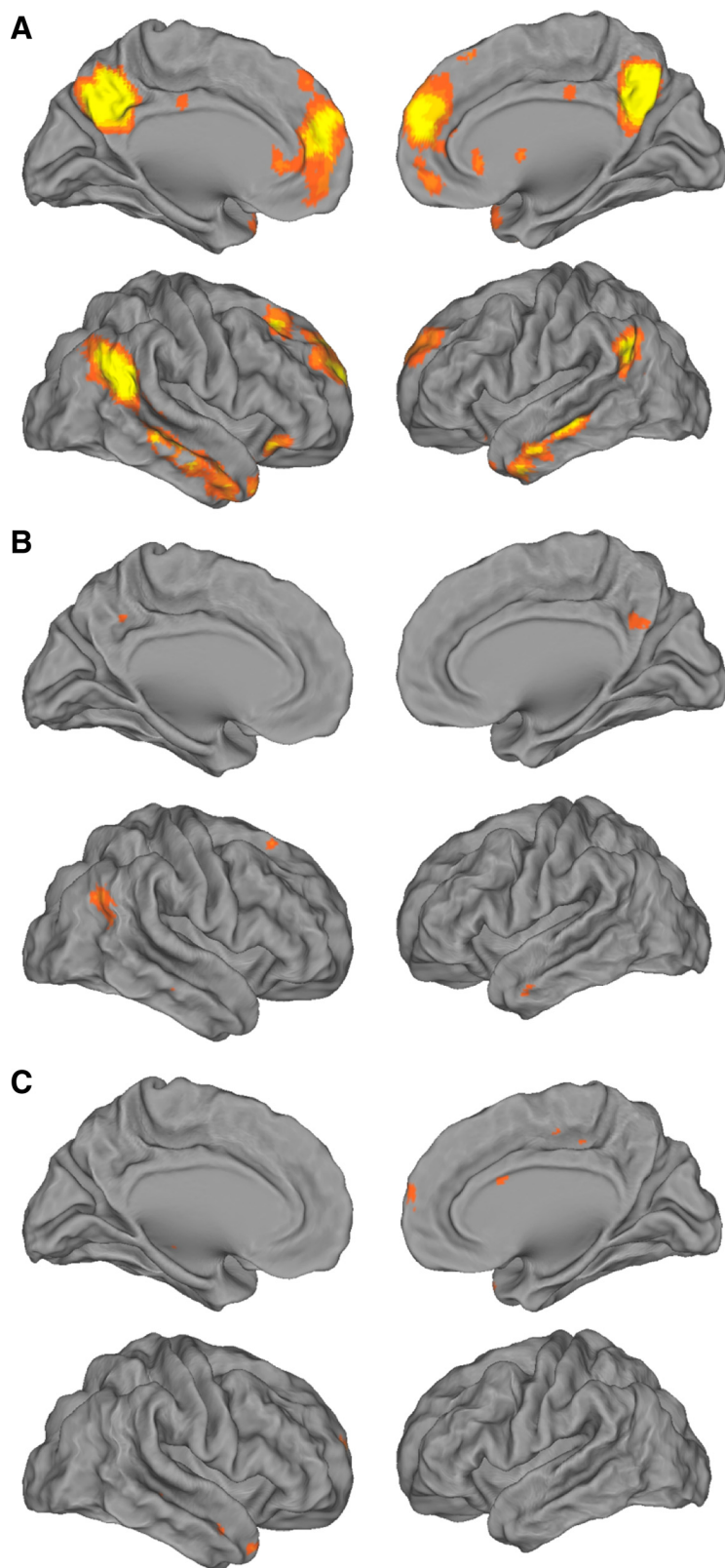


Figure 5. *A, B*, Regions showing significantly greater BOLD response to false belief–false photograph stories during the false belief task (corrected $p < 0.05$), separately for younger (*A*) and older (*B*) adults. Coordinates are displayed in Table 3. *C*, A direct comparison of these effects across age groups revealed that young participants showed significantly greater activation than older adults in dorsal medial prefrontal cortex.

plays of moving shapes that younger adults naturally interpret as mental agents (as during the animate movement task; Heider and Simmel, 1944; Martin and Weisberg, 2003).

These results stand in contrast to earlier work that has reported comparable levels of MPFC activation in older and younger adults (Gutchess et al., 2007a; Leclerc and Kensinger, 2010). For example, Gutchess et al. (2007a) observed similar response in ventral MPFC when older and younger participants were asked to reflect on their own personality characteristics. Leclerc and Kensinger (2010) observed a greater response in ventral MPFC when older versus younger participants considered emotional stimuli. Interestingly, in both investigations, these differences occurred in a region of MPFC substantially more ventral than that observed in the current study. This pattern suggests the intriguing possibility that aging may be associated with declines in dorsal, but not ventral, MPFC functioning. Future research designed specifically to investigate this possibility would be of great service in determining the precise effects of normal aging on MPFC function.

Earlier attempts to examine the question of how normal aging might affect social cognition have yielded contradictory results, such that some studies have reported no age-related changes in mentalizing (Happé et al., 1998; Castelli et al., 2010), whereas others have reported moderate declines over the lifespan (Maylor et al., 2002; Sullivan and Ruffman, 2004). Some research has suggested that mentalizing performance declines independently from well documented declines in fluid intelligence abilities (Maylor et al., 2002; Sullivan and Ruffman, 2004), although other researchers have argued that aging-related declines in mentalizing are mediated by intelligence and information-processing speed (German and Hehman, 2006; Charlton et al., 2009). The current study helps resolve these discrepancies by the use of a battery of social-cognitive tasks and a combination of performance and neural measures of mentalizing. Together, the current results strongly suggest that normal aging includes a decline in the social-cognitive skills linked to understanding other minds, and that this decline may be distinct from general aging-related cognitive declines (Maylor et al., 2002).

To the best of our knowledge, only one other study has examined the neural basis of mentalizing in older adults (Castelli et al., 2010). Interestingly, these authors report no aging-related deficits in perfor-

Table 3. Peak voxel and cluster size for all regions obtained from the contrast of false belief–false photo stories in the false belief task

Anatomic label	x	y	z	Peak <i>t</i>	Voxel extent
Young adults					
Dorsal medial prefrontal cortex	14	65	22	6.83	5608
	4	59	26	6.83	
	10	59	16	6.64	
Caudate nucleus	4	5	2	4.45	72
Midcingulate gyrus	0	−19	36	3.93	74
Superior temporal sulcus	−66	−25	−8	6.23	774
	−52	1	−36	5.17	
Temporoparietal junction	−60	−59	34	8.16	1237
	−46	−65	50	3.42	
	60	−51	26	8.52	4420
	54	−45	18	8.02	
Superior temporal sulcus	62	−23	−14	5.89	
Precuneus	−2	−59	38	10.43	3389
Cerebellum	0	−57	46	9.74	
	−26	−79	−34	4.43	95
Older adults					
Temporoparietal junction	48	−57	30	4.52	429
	46	−49	24	4.39	
	50	−55	18	3.82	
Precuneus	12	−53	30	3.98	113
Young versus older					
Dorsal medial prefrontal cortex	14	65	18	4.27	111
Older versus young					
Middle frontal gyrus	−36	39	20	3.19	62
Posterior insula	−30	−15	16	3.83	154

Stereotaxic coordinates reported according to the Montreal Neurological Institute coordinate system.

mance on the “reading-the-mind-in-the-eyes test,” and no difference in the default network between younger and older adults. Currently, it is unclear why this earlier research did not observe a comparable downregulation of MPFC as the current study. One possibility is that these earlier researchers used a form of the reading-the-mind-in-the-eyes test designed to be maximally easy (by using foil answers that were pretested to be least applicable to the stimuli). Accordingly, the performance of both younger and older adults was nearly perfect, a pattern that may obscure age-related declines in mentalizing performance. More intriguingly, older adults in this earlier study also engaged the lateral prefrontal cortex, an additional set of brain regions not typically associated with social cognition. These findings may suggest that older adults can bring to bear additional cognitive resources (i.e., those not typically associated with mentalizing) to perform the reading-the-mind-in-the-eyes task (Logan et al., 2002). This possibility suggests that older adults may successfully mentalize about others to the extent that they can use compensatory strategies that augment their otherwise impaired social-cognitive processing (Park and Reuter-Lorenz, 2009). At present, this hypothesis remains merely speculative, and future work will be needed to test these possibilities directly.

The existing literature on social cognition in healthy aging suggests one other possibility that might account for the lower performance observed in older adults during social cognition. Hess et al. (2001) suggested that older adults may be less motivated than younger adults to perform accurately on social-cognitive tasks. Older adults show less impaired performance on social tasks when told that they will be evaluated for social information about age-matched targets than for information about young people. These results suggest that older adults may be relatively capable of performing social-cognitive tasks accurately, but may be less motivated to do so. This possibility is supported

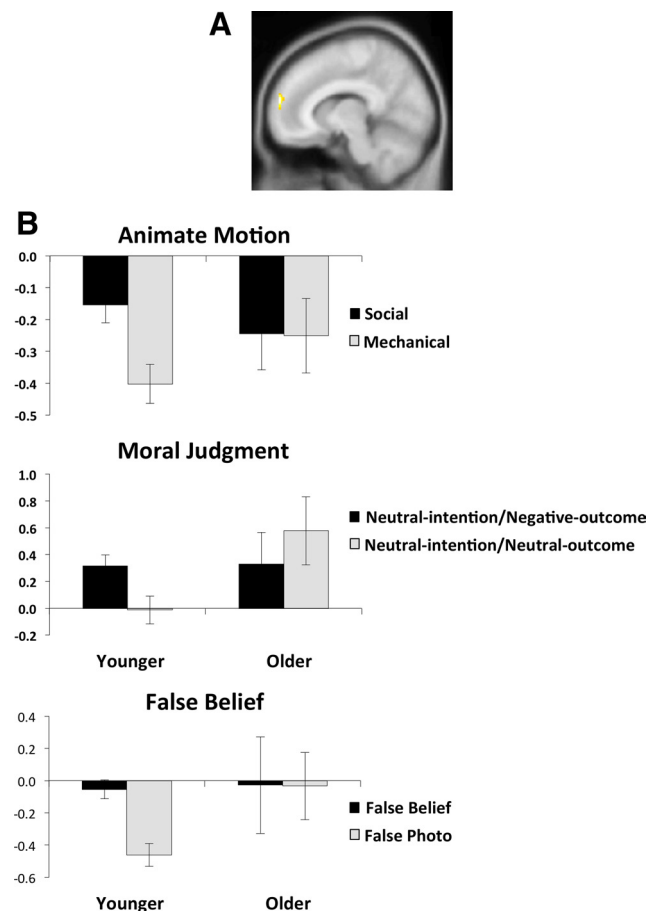


Figure 6. *A*, A conjunction across tasks revealed that a single region in dorsal medial prefrontal cortex responded differently in younger and older adults during social and nonsocial processing. This conjunction was performed by first identifying regions that showed greater response in younger than older adults for the contrast of social–nonsocial in each task and then creating a composite image that identified voxels common across tasks (see Materials and Methods). *B*, Parameter estimates for each condition of each task were extracted from this region of interest independently for younger and older adults, and are displayed for illustrative purposes.

by a good deal of work suggesting that older adults are motivated by different forms of social engagement. For example, more than young people, they may be more interested in maintaining a small number of high-quality relationships than in developing a large number of less intense ones (Carstensen, 1992; Mather and Carstensen, 2005). Perhaps the kinds of social-cognitive paradigms used in standard experimental psychology tasks simply do not sufficiently interest older adults, especially to the extent that they typically use unfamiliar individuals with whom older adults may be less motivated to engage socially. The possibility that aging may represent a shift in social motivation is intriguing, but given the small number of studies on the nature of social cognition in normal aging, this speculation awaits considerable further investigation.

Finally, one caveat of the present study is that we did not measure older adults' performance on general cognitive abilities (such as working memory or cognitive control). To the degree that our tasks were able to isolate social-cognitive functioning from general cognitive functioning, we are confident that older adults' performance deficits in social-cognitive tasks were not attributable to more general cognitive declines. However, it is possible that declines in general cognitive performance may have contributed to declines in social-cognitive performance.

Overall, the current results suggest that aging is associated with a decline in mentalizing, as indexed by performance across different social-cognitive tasks as well as downregulation of neural regions associated with social cognition—specifically, dorsal aspects of the MPFC. Differences between younger and older adults were robust across varying levels of working memory and verbal-processing demands, were not observed in nonsocial versions of the same tasks, and were not ameliorated by providing older adults with explicit cues to represent mental states. Such work contributes to the important goal of characterizing the complete arc of cognitive development over the full course of the lifespan.

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